

SUZUKI AWARD**Risk sensitivity of a forager with limited energy reserves in stochastic environments**Hiromu Ito^{1,2,3}¹Department of General Systems Studies, The University of Tokyo, Tokyo, Japan²Department of International Health, Institute of Tropical Medicine, Nagasaki University, Nagasaki, Japan³Department of Environmental Sciences, Zoology, University of Basel, Basel, Switzerland**Correspondence**

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Abstract

Long-term environmental stochasticity is known to affect the adaptive evolution of life history traits. In stochastic environments, there are two different levels of behavioral optimization, as follows: Level 1, the optimal strategy under an intra-generation stochastic environment and Level 2, the optimal strategy under an inter-generation stochastic environment. This article presents a simple optimal foraging model under predation risks and verified the effect of behavioral optimization on the foraging time ratio. In this model, foragers are exposed to predation risks during foraging but are safe if they stay in their nests without any food. The foraging time allocation strategies that optimize the geometric mean fitness (Level 2) were compared with the arithmetic mean fitness (Level 1) to verify the effects of intergenerational stochasticity, whereby there is an alternation in good/bad environments across generations. As in previous studies, risk-averse strategies (a shorter foraging time is adopted for Level 2 than for Level 1) were commonly observed using this model. Unexpectedly, the model showed a tendency toward a preference for risk-prone strategies. This qualitative difference became prominent when food was abundant and the maximum energy reserves were small. Theoretical studies have shown that risk-averse strategies are commonly adopted during food shortages and result in starvation. However, the current results indicate that risk-prone strategies may become optimal under a limited reserve capacity. Thus, the optimal strategy depends not only on the individual status and environmental conditions, but also on the detailed selection regimes.

KEYWORDS

adaptive behavior, foraging theory, geometric mean fitness, mathematical modeling, optimal behavior

1 | INTRODUCTION**1.1 | Optimal foraging theory**

Optimal foraging theory under predation risk has been extensively studied in the fields of ecology and evolution (Houston, Higginson, & McNamara, 2011a, 2011b; McArthur, Banks, Boonstra, & Forbey, 2014; Stephens,

Brown, & Ydenberg, 2007; Stephens & Krebs, 1986). Of particular interest has been foraging behavior in environments characterized by uncertain amounts of food and predator abundance (Caraco, 1980; Houston & McNamara, 1999; Real & Caraco, 1986; Stephens et al., 2007; Stephens & Krebs, 1986). In fact, it has been found that the foraging behavior of many animals (e.g., birds and fish) is strongly influenced by predation risks and variations in food quality and quantity (Caraco, Martindale, & Whittam, 1980; Fraser,

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Gilliam, Akkara, Albanese, & Snider, 2004; Greenwood & Metcalfe, 1998; Jones & Rydell, 1994; Krams, 2000; Lima, 1985, 1988a, 1988b; Metcalfe, Fraser, & Burns, 1999). In addition, the reduction in foraging time in the presence of predators is likely to lead to a long-term decrease in reproduction (Lima, 1998; Martin & Lopez, 1999). Because benefits (e.g., food amount) and risks (e.g., predation and starvation) can be analyzed using models, optimal foraging theory is a good base from which the decision-making mechanism of all foraging organisms can be understood.

1.2 | Arithmetic and geometric mean fitness

The response to stochasticity, whereby foraging efficiency is maximized and risk is minimized, applies to all organisms (Houston et al., 2011a, 2011b; Stephens & Krebs, 1986; Yoshimura & Clark, 1991). Hence, the best strategy should take unpredictability into account. When environmental conditions are temporally or spatially heterogeneous, the average (mean) fitness is measured via two typical methods, the arithmetic mean and the geometric mean. The arithmetic mean is an appropriate measure of the fitness when the environmental fluctuation occurs within an individual lifetime only. On the other hand, the geometric mean is an appropriate measure when the environment fluctuates temporally across generations (Cohen, 1966; Lewontin & Cohen, 1969; Schaffer, 1974; Stearns, 1976; Yoshimura & Clark, 1991).

Here, I define two different levels of behavioral optimization, as follows: the optimizations that do not consider (Level 1) or consider (Level 2) intergeneration stochasticity. Accordingly, Level 1 should be measured using the arithmetic mean, and Level 2 should be measured geometrically because of cross-generational environmental variations (i.e., good years or generations vs. bad years or generations).

1.3 | Risk sensitivity and risk aversion

Much previous work has indicated that “risk-averse” behaviors are common in nature and theory (Stephens et al., 2007; Stephens & Krebs, 1986; Yoshimura, Ito, Miller III, & Tainaka, 2013a; Zhang, Brennan, & Lo, 2014). In our previous model of risk-sensitive foraging, we found a preference for a “risk-prone” strategy when the foraging time is longer than optimal foraging time that maximizes the arithmetic mean fitness (x_A^*) (Ito, Uehara, Morita, Tainaka, & Yoshimura, 2013). In the same way, we found a preference for a “risk-averse” strategy when the foraging time is shorter than (x_A^*). Note that, in both the present model and our previous model, a risk-neutral strategy is defined as the ratio of foraging time when maximizing foraging efficiency (Ito et al., 2013). A risk-prone strategy is when a forager extends his/her foraging time under predation risk from a risk-neutral strategy. In contrast, a risk-averse strategy is when a forager shortens his/her foraging time from a risk-neutral strategy (Houston & McNamara, 1999; Mangel & Clark, 1986,

1988). In this sense, we define risk neutral as the ratio of foraging time when maximizing the arithmetic mean fitness (x_A^*), because (x_A^*) is the optimal strategy to maximize the expected value of Level 1. Thus, if foraging time is longer or shorter than this risk-neutral strategy (x_A^*), risk-prone and risk-averse strategies can be discriminated as follows (Ito et al., 2013):

Case 1: Risk-averse (optimal foraging time of Level 2 < Level 1; $x_G^* < x_A^*$).

Case 2: Equivalently risk-sensitive (optimal foraging time of Level 2 = Level 1; $x_G^* = x_A^*$).

Case 3: Risk-prone (optimal foraging time of Level 2 > Level 1; $x_G^* > x_A^*$).

Our previous foraging model also revealed this risk-averse tendency in optimal foraging behavior (Ito et al., 2013). Notably, risk-prone strategies appeared in extreme conditions under which gambling was necessary to achieve any reproductive success. In this model, the effects of stochastic environments on the risk sensitivity of foragers were evaluated using the difference between the geometric mean fitness and the arithmetic mean fitness. However, such a model ignores the capacity of the maximum energy reserves that are inherent in any foraging animal (Caraco et al., 1980; Whelan & Brown, 2005). Thus, in the present study, the same model was used, but with the inclusion of the maximum energy reserves of a forager, to determine whether the overall differences were the same as those described by our previous model (Ito et al., 2013).

1.4 | State variable and optimal behavior

Predator avoidance behavior and foraging time allocation depend on specific “states”, such as body size (Clark & Mangel, 2000; Lima, 1998; Rizzuto, Carbone, & Pawar, 2017). Individual status, such as body size or fat reserve, has been included as a state variable in dynamic programming (DP) studies of animal behavior (Clark, 1987; Houston, Clark, McNamara, & Mangel, 1988; Houston & McNamara, 1999; Mangel & Clark, 1988). Note that in DP, the overall objective function is maximized at every time step. Therefore, the optimal solutions depend on the state variables. However, most DP problems cannot be solved due to the large computation load (Merkuryev, 2012). In addition, DP models cannot be used to compare optimality at the average offspring level (Level 1) with that at the extinction probability level (Level 2).

In the present study, I considered not only the environmental stochasticity of the amount of food and predation risk, but also the capacity of the maximum energy reserves. A DP model was not used, primarily to simplify the model, but also to avoid difficult qualitative analysis. A simple foraging model was built and the effects of short-term and long-term environmental changes on optimal foraging

strategies were verified. This model was built with consideration to the fact that energy reserves have a strong effect on bad environments when they become a critical factor for survival. The importance of this model is that the optimization of the average number of offspring (Level 1) seems to have a strong effect on the minimization of extinction probability (Level 2), because it becomes critical for all individuals of a generation in bad environments, often leading to extinction (Ito et al., 2013). This model can help us to understand not only the effect of short-term and long-term stochastic environments (food quantity and predator abundance) but also the effect of the maximum energy reserves of individuals. This work will also help to generalize foraging theory through the integral analysis of state variables and environmental conditions.

2 | MODEL

A simple foraging-time-allocation model that optimizes foraging efficiency under various predation (death) risks and food amounts was built. The foragers (decision-makers) are assumed to be subject to a risk of predation during foraging, while the time that they spend in a safe nest (the time during which no foraging acts are performed) is completely free from predation (Ito et al., 2013; Lima, 1985; Lima, Valone, & Caraco, 1985; Stephens & Krebs, 1986; Yoshimura & Clark, 1991). In this model, a_i is the food amount, and b_i is the abundance of predators in the i -th environment. The foragers within a generation are assumed to experience one of two typical environments ($i = 1, 2$) with a given probability (i.e., $p_1 + p_2 = 1$). The first environment ($i = 1$) is a good environment with fewer predators, whereas the second environment ($i = 2$) is a bad environment with more predators (i.e., $[b_1 = 3] < [b_2 = 10]$). The ratio of foraging time was set as x ($0 \leq x \leq 1$), during which predation occurs randomly. In the current model, the foraging time (x) is the proportion of the lifetime allocated to foraging behavior when the total lifespan is set to 1. For example, when the ratio of foraging time is $x = 0.5$, a forager devotes half of its entire lifespan to foraging behavior. Note that during $(1 - x)$, foragers stay in the safe nest, with no predation risk. From this assumption, the survival rate [$S_i(x)$] in environment i follows a Poisson distribution ($e^{-b_i x}$) (Ito et al., 2013; Lima, 1985; Lima et al., 1985), as shown in Equation (1) (Figure 1a):

$$S_i(x) = e^{-b_i x} \quad (1)$$

Although the amount of food acquired increases monotonically with x , the intake efficiency (digested food amount) decreases asymptotically as it approaches a certain value [r ($0 << r$)], at which point the energy reserves of the forager are full (Whelan & Brown, 2005) (Figure 1b). The food gain $F_i(x; a_i)$ during a foraging time of x is expressed as follows:

$$F_i(x; a_i) = r \left(1 - e^{-\frac{a_i}{r} x} \right) \quad (2)$$

The fitness [$\varphi_i(x)$] in a single environment is then given by the following equation:

$$\varphi_i(x) = F_i(x; a_i) \cdot S_i(x) = r \left(1 - e^{-\frac{a_i}{r} x} \right) \cdot e^{-b_i x} \quad (3)$$

This is a simple foraging model with a basic trade-off between food gains and predation risks. The fitness curves of the current model can be drawn based on any three parameters (i.e., a , b and r) (Figure 1c,d). Even if a large amount of food is available in the environment, the amount of food intake is not simply proportional to the available amount of food but is instead limited by the maximum energy reserves of a forager. The optimal foraging time (x^*) under a stable (single) environment is derived from Equation (3), as follows:

$$x_i^* = -\frac{r}{a_i} \left\{ \log \left(\frac{b_i r}{a_i + b_i r} \right) \right\} \quad (4)$$

x^* decreases as the amount of food (a) and/or predator abundance (b) increases and increases as the maximum energy reserve (r) increases (Figure 2) (Stephens & Krebs, 1986).

3 | RESULTS

The arithmetic mean fitness (A) and geometric mean fitness (G), given by the following formulas, were compared:

$$A(x) = p_1 \varphi_1 + p_2 \varphi_2 = \sum_{i=1,2} p_i \varphi_i \quad (5)$$

and

$$G(x) = \varphi_1^{p_1} \varphi_2^{p_2} = \prod_{i=1,2} \varphi_i^{p_i} \quad (6)$$

Note that $A \geq G$ for any foraging time (x). Neither the maximum A [$A^* = A(x_A^*)$] nor G [$G^* = G(x_G^*)$] can be solved analytically and are evaluated numerically by calculating the derivatives: $\frac{dA}{dx} = 0$ and $\frac{dG}{dx} = 0$.

The effect of stochastic environments on foraging time allocation was assessed in terms of the two environmental conditions, namely, the amount of food (a_i) and the abundance of predators (b_i ; $i = 1, 2$) (Figure 1c,d). The fitness functions of the arithmetic mean fitness (A) and the geometric mean fitness (G) are plotted under the assumption that environments E_1 (good) and E_2 (bad) occur with equal probability (i.e., $p_1 = p_2 = 0.5$) (Figure 1c,d). The maximal (peak) points are shown for the arithmetic mean fitness and the geometric mean fitness. When the optimal foraging time of the geometric mean fitness (x_G^*) is less than that of the arithmetic mean fitness (x_A^*) (i.e., $x_G^* < x_A^*$), a “risk-averse” strategy is more strongly preferred (Figure 1c),

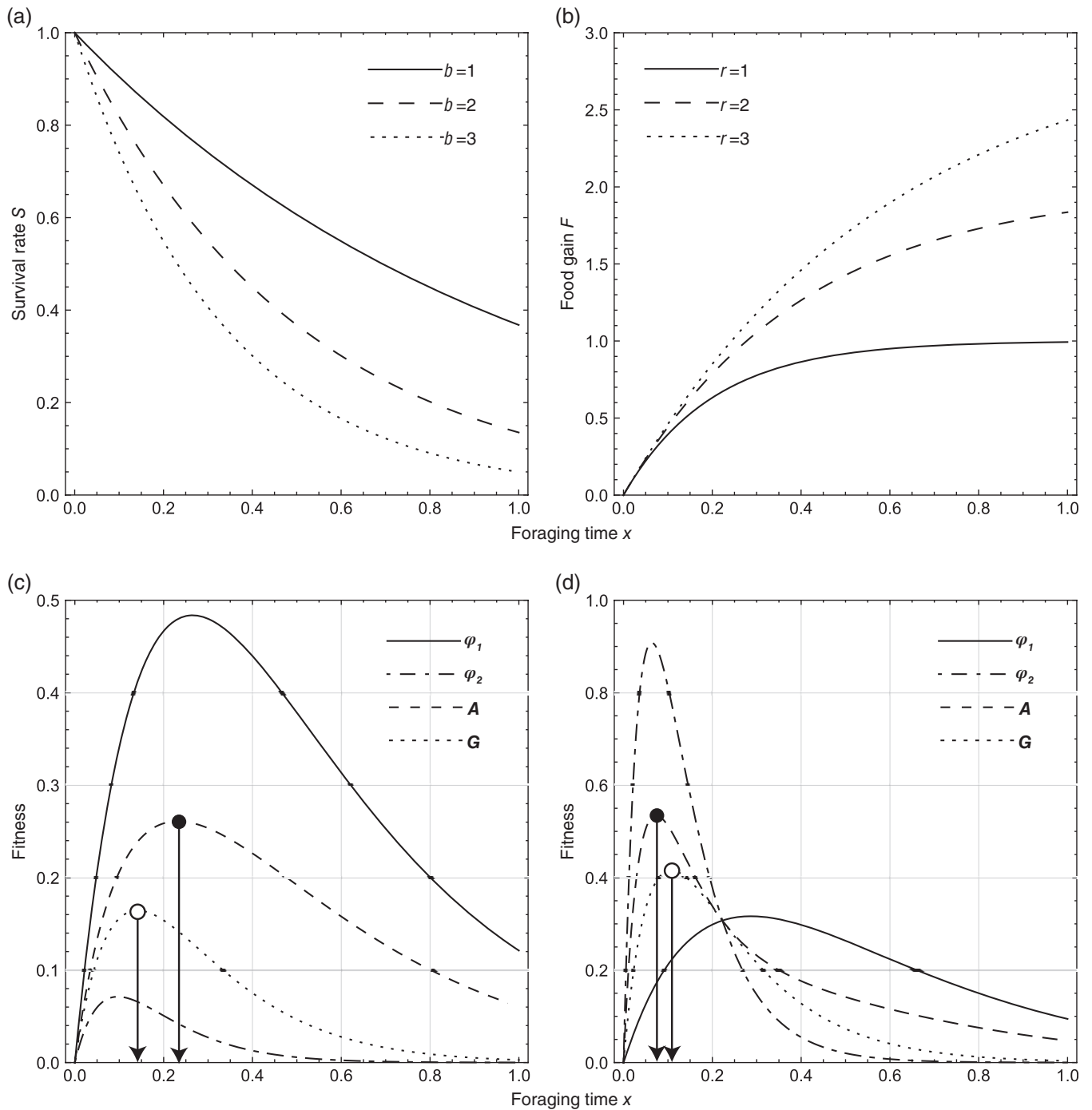


FIGURE 1 (a, b) Graphics of Equations (1) and (2). (a) The curve of the survival rate $S(x)$ for various predator abundances ($b = 1, 2$ and 3). (b) The curve of food gain $F(x; a)$ for various maximum energy reserves ($r = 1, 2$ and 3) with a constant amount of food $a = 5$. (c, d) Fitness function for foraging time allocation in stochastic environments. Potential fitness functions of a good environment, E_1 , and a bad environment, E_2 (i.e., $b_1 = 3, b_2 = 10$), such as φ_1 and φ_2 , and their corresponding arithmetic mean fitness (A ; dashed line) and geometric mean fitness (G ; dotted line) are plotted against foraging time (x) ($x = 0, \dots, 1$). The probabilities of E_1 and E_2 are set to be equal, and the maximum energy reserves are kept constant (i.e., $p_1 = p_2 = 0.5, r = 3$). The available amount of food for good/bad environments are set as follows: (c) $a_1 = 5, a_2 = 2$ and (d) $a_1 = 3, a_2 = 40$. Open circles represent the optimal (peak) points for the geometric mean fitness, and the filled circles represent the optimal (peak) points for the arithmetic mean fitness

whereas when the opposite situation occurs (i.e., $x_G^* > x_A^*$), a “risk-prone” strategy is more strongly preferred (Figure 1d).

The differences in the optimal foraging time between the arithmetic mean fitness (x_A^*) and the geometric mean fitness (x_G^*) are shown in Figures 3 and 4. The risk-prone

strategy can be observed in a wider region when the amount of food is high and r is small (Figure 3a,b; Figure 4a,b). The largest difference in the two optimal strategies (x_G^* and x_A^*) is found when the r is large and the amount of food in both good and bad environments (a_1 and a_2) is small.

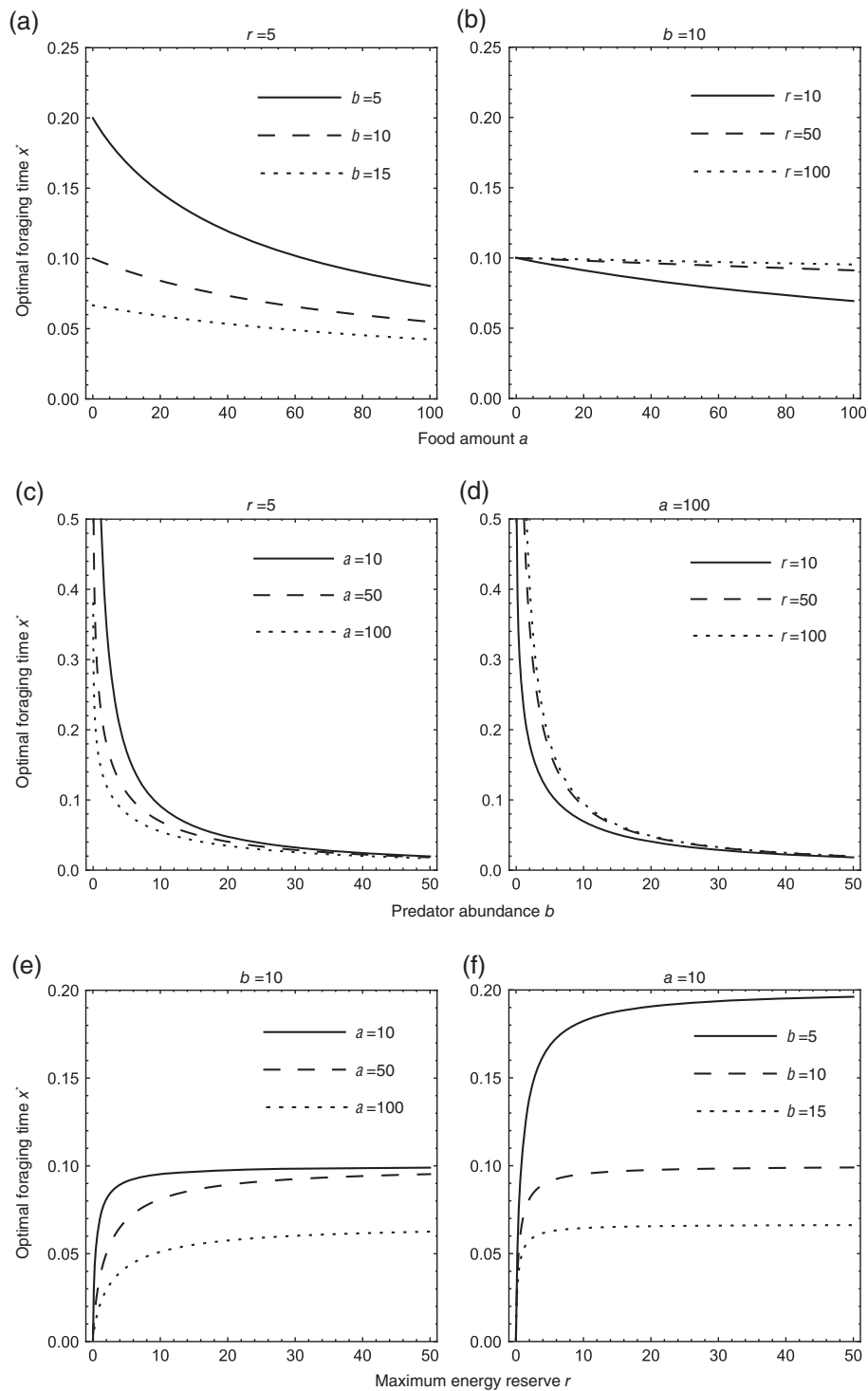


FIGURE 2 Effects of maximum energy reserves (r), available amounts of food (a), and the number of predators (b) on the optimal strategy (x^*) in a single generation. (a, b) Optimal foraging time (x^*) versus the amount of food (a) for various predator abundances ($b = 5, 10$ and 15) and maximum energy reserve ($r = 10, 50$ and 100). (c, d) Optimal foraging time (x^*) versus predator abundance (b) for various amounts of food ($a = 10, 50$ and 100) and maximum energy reserve ($r = 10, 50$ and 100). (e, f) Optimal foraging time (x^*) versus the maximum energy reserve (r) for various amounts of food ($a = 10, 50$ and 100) and predator abundances ($b = 5, 10$ and 15)

4 | DISCUSSION

Optimal foraging theory is an important topic because it enables us to understand decision-making mechanisms from benefits and risks. To promote our understanding of optimal decision-making theory, this model considered not only the

balance between profits and risks, but also individual status. Our previous results regarding risk sensitivity showed a risk-averse tendency in environments with an abundance of food (Ito et al., 2013). However, the present study shows that introduction of maximum energy reserve into the model increases the risk-prone tendency compared to our previous

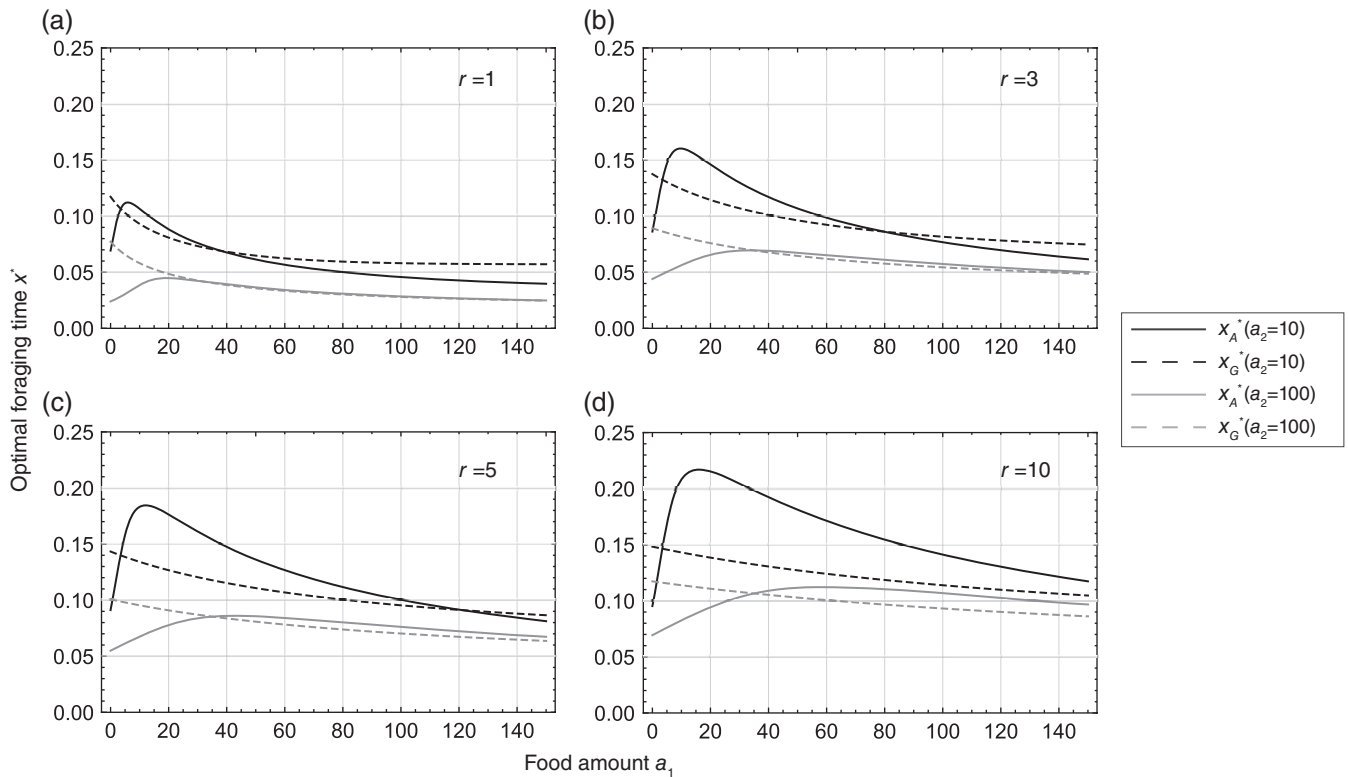


FIGURE 3 Risk-sensitivity analyses of foraging time allocation. The optimal foraging time (x^*) in stochastic environments (x_A^* : solid line; x_G^* : dashed line) versus the available amount of food in E_1 such as $a_1 = 0, \dots, 150$ for various amounts of food in E_2 , such as $a_2 = 10$ (black line) and $a_2 = 100$ (gray line). The other parameters are kept constant (b_1, b_2) = (3, 10). (a) $r = 1$, (b) $r = 3$, (c) $r = 5$ and (d) $r = 10$

model. By introducing one simple limitation in the present model (i.e., the maximum energy reserves), it was found that optimality at the average number of offspring level (Level 1) and that at the minimization of extinction probability level across generations (Level 2) are reversed (from risk-averse to risk-prone) under some environmental conditions (i.e., when the amount of food is high and maximum energy reserve is small). The current results demonstrate that the relationships of risk-prone and risk-averse strategies can be reversed when maximum energy reserves are introduced. Thus, the detailed setting for such limitations may drastically change the optimality of the dynamic solutions.

The current model is a simple model of optimal foraging in stochastic environments over generations that incorporates food intake and maximum energy reserves. In the previous model, which ignored maximum energy reserves (and implied an infinitely large energy reserve), risk-prone strategies were limited in areas and locations in the parameter space (see the case of a large r in Figure 4d) (Ito et al., 2013). However, the utility of food does not exhibit a simple proportional relationship with the amount of food; instead, it depends on the maximum energy reserves and the degree of starvation (Caraco, 1980; Caraco et al., 1980; Real, 1980a, 1980b). In the current model, which included maximum energy reserves, risk-prone strategies appear in much wider areas and on the opposite sides from the previous model (Figure 4a–c). The reason for the expansion of a risk-prone strategy with the inclusion of maximum energy reserves

could be the necessity of frequent foraging because of small energy reserves (Figure 1d).

The current model is similar to some previous ones in terms of the foraging theory, which consider the stomach condition of decision-maker. For example, Clark also examined the effect of capacity in stochastic environments (Clark, 1987). Moreover, earlier models have indicated that a risk-prone strategy is more likely to occur when organisms are hungry (Houston et al., 1988). The work of these authors further shows that smaller energy reserves imply a higher probability of suffering starvation. However, this previous work did not comprehensively treat the level of adaptation (i.e., Level 1–2), which means what kind of environmental situations and individual conditions diverge Level 1 and 2 from each other. Specifically, they analyzed foraging behavior using DP. In contrast, I used a mathematical analysis rather than a numerical approach such as DP; I not only analyzed the effect of state variable (maximum energy reserve) of the decision-maker, but also mathematically showed the gap in optimal strategies between Level 1 and Level 2 behavioral optimization. Indeed, for the first time, a mathematical distinction between Levels 1 and 2 was applied to foraging theory in the current model.

Many studies have shown that risk-averse foraging behavior is generally promoted under broad conditions except for severe situations, such as extreme cold or starvation (Caraco & Chasin, 1984; Ito et al., 2013; Yoshimura & Shields, 1987). However, several empirical studies have

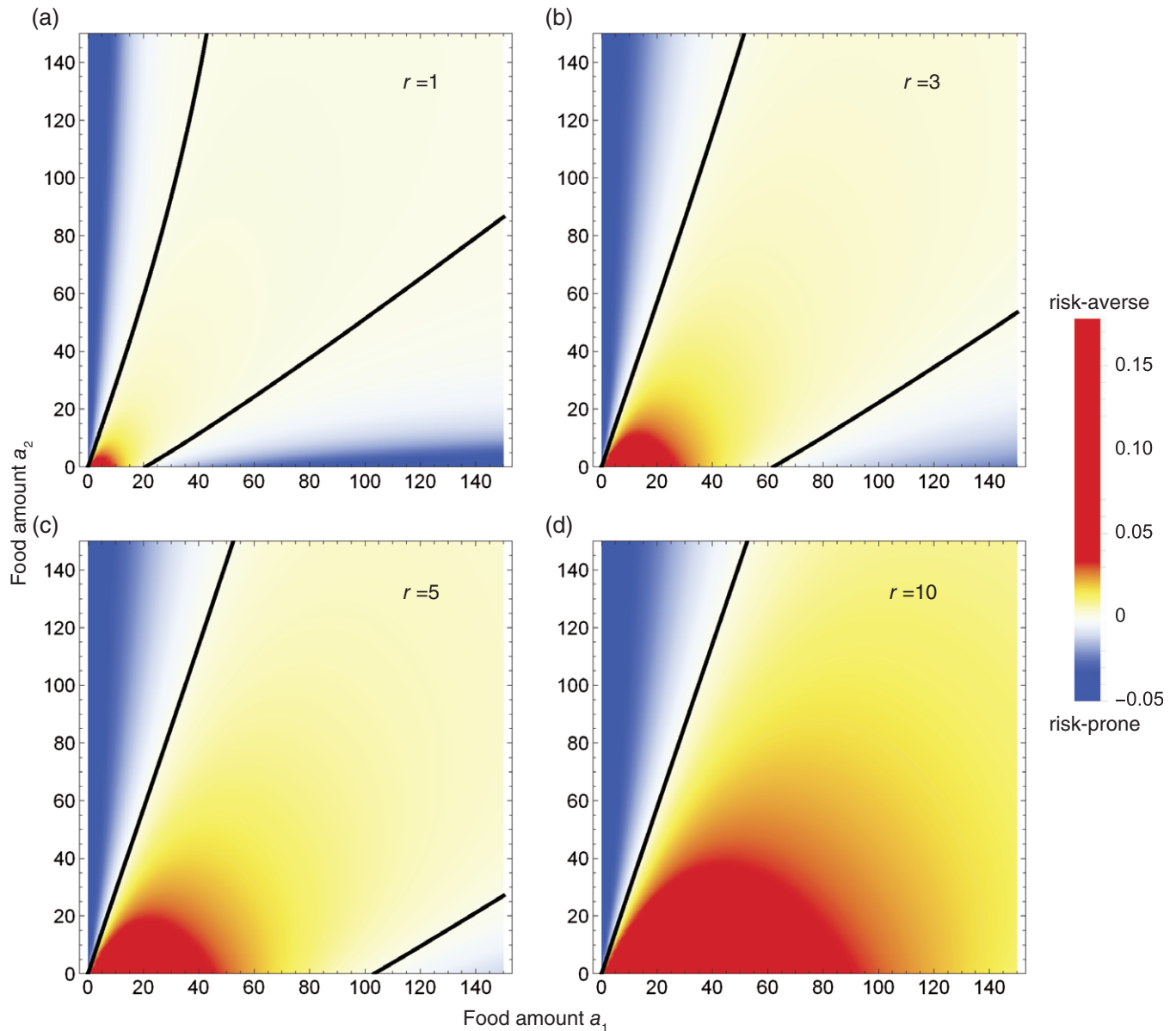


FIGURE 4 Phase plane of the difference between the arithmetic and geometric optimal foraging times ($x_A^* - x_G^*$) plotted against food abundances of a_1 and a_2 . In the red regions, the strategies become risk-averse (e.g., $x_A^* > x_G^*$), while in the blue regions, the strategies become risk-prone (e.g., $x_A^* < x_G^*$). The solid line indicates neutral boundaries for risk sensitivity ($x_A^* = x_G^*$). The probabilities of E_1 and E_2 are set as equal (i.e., $p_1 = p_2 = 0.5$), and the predator abundance is kept constant ($b_1 = 3, b_2 = 10$). (a) $r = 1$, (b) $r = 3$, (c) $r = 5$ and (d) $r = 10$

observed risk-prone behavior in a variety of animals, including birds (Caraco et al., 1980), fish (Sih, 1994), insects (Frank & Eduard Linsenmair, 2017; Moses & Sih, 1998), squirrels (Bowers & Breland, 1994), chimpanzees (Gilby & Wrangham, 2007) and humans (Coddington, Bliege Bird, & Bird, 2011). The current results support this previous work and imply that risk-prone behavior is far more common than expected and may be invoked by certain biological limitations, such as the maximum energy reserves. In this sense, optimal solutions may be affected by many other limiting factors, such as variation in the reduction of digestive rates under conditions of a full/empty stomach or good/bad health (Armstrong & Schindler, 2011), niche breadth and nutrient value (Dussutour, Latty, Beekman, & Simpson, 2010; Houston et al., 2011a, 2011b; Mayntz, Raubenheimer, Slomon,

Toft, & Simpson, 2005). More importantly, the directions and trends of risk sensitivity may be reversed if certain explicit factors, such as the amount of fat reserve and the amount of wealth in humans, are introduced. Further research using theoretical models is needed, and theoretical predictions should be verified using empirical systems, as in traditional risk-sensitivity analyses of an individual.

This model cannot explain all real-world risk-prone foraging behavior. For example, the chimpanzee's (*Pan troglodytes schweinfurthii*) risk-prone foraging (hunting) behavior has not been explained by the traditional foraging models that focus on the starvation threshold (Gilby & Wrangham, 2007). Indeed, chimpanzees adopt risk-prone behaviors even when they already have a high diet quality. However, the current model may be able to verify the relationship between the body size

and the foraging behavior. As the body size can be defined as the maximum energy reserve, the current model can demonstrate risk sensitivity differences between large and small organisms. Indeed, several studies have shown that risk sensitivity of foraging behavior differs depending on body size. Namely, small animals (such as yellow-eyed juncos, bumblebees and 15-spined sticklebacks) adopt more aggressive foraging behavior, and large animals (such as coyotes, bobcats and lions) adopt more conservative foraging behavior (Caraco et al., 1990; Carter & Dill, 1990; Croy & Hughes, 1991; Kissui & Packer, 2004; Odonoghue, Boutin, Krebs, & Hofer, 1997).

Risk-sensitivity is not only affected by body size (maximum energy reserve), but also lifespan and life history (Kolodny & Stern, 2017). Large and small organisms have different life histories, such as lifespan and the number of reproduction events. Kolodny and Stern (2017) have argued that the number of decision-making events in an individual's lifetime is also an important factor to consider when assessing risk preference. In other words, risk-averse strategies are advantageous if there has only been one decision-making event in an organism's lifetime; however, the advantage of choosing a risk-averse strategy diminishes as the number of decision-making events increases. This means that organisms with many reproduction events in their life history are more likely to exhibit a risk-prone strategy. The authors concluded that evolution of risk preference is determined by "reproduction dynamics", "life history" and "population size". In this sense, although our model can be mathematically analyzed, we should build an agent-based simulation model when considering the life history of an organism.

We should also note that the maximum energy reserve is also largely involved in reproduction dynamics of long-lived organisms (Bårdsen, Næss, Tveraa, Langeland, & Fauchald, 2014); long-lived organisms experience a temporally varying cost of reproduction and build body reserves during periods of favorable environmental conditions. They prepare for reproduction by using these reserves as a buffer against periods of unfavorable conditions; this is true for humans (Lummaa & Clutton-Brock, 2002), large herbivores (Grailland & Yoccoz, 2003), birds (Hanssen, Hasselquist, Folstad, & Erikstad, 2005), fish (Klemetsen et al., 2003) and reptiles (Radder, 2006). Therefore, the introduction of the concept of maximum energy reserve to the foraging model means that complex interactions of this variable with various other elements become apparent.

In this sense, the present model is still a simple model that ignores many important features of optimal foraging. For example, the analysis of individual states is insufficient because the nonlinearity of fitness consequences is not included. Namely, in this model, the amount of food intake is assumed to be equal to the fitness gain of an individual. However, both the expected utility theory (Caraco, 1980; Caraco et al., 1980; Real, 1980a, 1980b) and dynamic utility theory (Ito, Katsumata, Hasegawa, & Yoshimura, 2016, 2017; Yoshimura et al., 2013a; Yoshimura, Ito, Miller III, & Tainaka, 2013b) suggest

that fitness consequences are not linearly associated with food intake. The introduction of utility functions (either static or dynamic) further complicates the calculations and analyses. However, in the future, the expected utility theory, which considers the individual status (current status) and food quality, may explain the mechanism underlying the occurrence of risk-prone foraging behavior (as seen in, e.g., chimpanzees) that cannot be explained by the traditional foraging theory. Thus, the optimality of risk-sensitive foraging is highly variable and depends on the detailed selection regimes, such as maximum energy reserve, predation risks and food availability.

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CONFLICTS OF INTEREST

The author declares that no potential conflict of interests.

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